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When a snail dies in the forest, how long will the shell persist? Effect of dissolution and micro-bioerosion

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Abstract: Snail shells persist in the environment after death, but we know little about the rate at which shells decompose. Assumptions about the rate of shell decomposition are relevant to conservation biologists who find empty shells or biologists using empty shells to make inferences about assemblages of living individuals. I put shells in 1.6 mm mesh litter bags (excluding macro-grazers) in Delaware and northern Michigan, U.S.A. and monitored shell mass annually for 7 years. Decomposition rates differed among species, but I found no difference in rates at two sites with different habitats. Surprisingly, loss of periostracum had no effect on shell decomposition rate. At the locations and habitats studied, decomposition rate of snails averaged 6.4% per year, excluding shells that broke during the experiment (shell half life = 11.5 years), or 10.2%, including shell breakage (half life = 7.5 years). Half lives would likely be shorter if macro-grazers had access to shells. These results caution us to draw conclusions carefully when including empty shells in inferences about assemblages of living individuals.

Key words: chemical weathering, death assemblage, decomposition rate, land snail, periostracum

After snails die, their shells persist in the environment. Although some shells survive as fossils for hundreds of millions of years, most shells decompose (or effectively disappear) more quickly than that, probably on the order of months or years. A shell in a dry, protected place such as a desert or a museum might persist for hundreds of years. A shell on the forest floor might persist more briefly—but how briefly?

Although we know little about the decomposition rates of land snail shells in leaf litter, many studies make assumptions about the rate of shell decomposition and could benefit from more information about the decomposition rates (Menez 2002). Management biologists making conservation decisions would find decomposition rates relevant for knowing how long ago a species was living at a site where an empty shell was found. Although using data from snails collected alive would give more reliable results, biologists conducting biodiversity surveys commonly use empty shells as an expedient way to indicate the presence of species at a site. Furthermore, since methods for recovering snails from leaf litter (*e.g.*, sieving and picking snails) are labor intensive, including information from empty shells is tempting for at least two reasons. First, empty shells can usually be recovered along with live specimens with little extra effort, and second, the only occurrence of rare species in a sample might be empty shells, so excluding empty shells would discard information. Studies in which empty shells and live shells are counted indiscriminately would, of course, overestimate population sizes of the living snails. Furthermore, if shell decomposition rates differ among species, then including dead shells would overestimate the abundance of robust-shelled species. Using empty shells to calculate proportions of species in the assemblage of living individuals requires assuming that the death assemblage accurately represents the assemblage of living individuals. This assumption might be incorrect if different species, robust and fragile-shelled, decompose at different rates or if shells at different sites decompose at different rates.

Shells of *Ovachlamys fulgens* (Gude, 1900) decomposed in an average of five months in Costa Rica during the dry season (Barrientos 2000). Aside from that study, most of what we know about the rate at which snail shells decompose is anecdotal. Welter-Schultes (2000) collected all the dead shells of *Albinaria jaeckeli* Wiese, 1989 that he could find in a particular area once in 1987 and again in 1990. The number of dead shells he collected was similar in each year, suggesting that the dead shells had been completely replaced within three years.

Shells probably disappear by three main processes: dissolution, breaking, and bioerosion (shell removal by grazing). Shells that are protected from bioerosion decompose more slowly than shells that are exposed to this process (Cadée 1999). Although consumption by larger organisms such as other snails and decomposition by crushing and breaking are real processes contributing to disappearance of shells, in this study I excluded macro-grazers larger than 1.6 mm and breakage (for most analyses) by keeping target snails in mesh bags. Consequently, the shell decomposition rates in this study are likely to be slower than in experiments allowing access by macro-grazers such as other snails. How-

ever, excluding macro-grazers allowed me to focus on the effects of dissolution and micro-grazers less than 1.6 mm that might remove shell material by grazing.

In this study, I address 4 questions: (1) Do shells of different species decompose at different rates, (2) Do shells in different habitat types decompose at different rates, (3) Does periostracum loss influence shell decomposition rate, and (4) What is the mean half life of a dead snail's shell?

MATERIALS AND METHODS

Localities and species

To address how long empty shells persist in the forest, and to test for differences in decomposition rates among species and among sites, I put individually numbered shells in mesh litter bags at sites of two different habitats in northern Michigan and at one site in Delaware with three replicates located about 15 meters apart at each locality. The litter bags were approx. 22 × 22 cm with 1.6 mm screen openings and held about 1 liter of soil, leaf litter, and the decomposing shells. The litter bags were placed on the mineral soil surface and covered with about 5 cm of leaf litter and a small amount of soil. I monitored shell mass annually for 7 years.

Measuring mass loss from material in mesh bags has been used in many studies of leaf litter decomposition (Taylor and Parkinson 1988) and is an applicable method to studying snail shell decomposition. Choice of mesh size in the bags is a trade-off between retaining fragments and allowing entrance by grazing organisms. If larger animals were important grazers on shells, then mesh sizes that exclude them will result in slower shell decomposition rates. For example, such a decrease in decomposition rate was observed in studies of leaf litter between larger mesh that admitted and smaller that excluded grazers (Cornelissen 1996).

The two northern Michigan localities included a mixed pine and hardwood forest on a sandy outwash plain and a mixed hardwood forest on rich moraine soil. At these localities, I used locally collected shells from near the sites where I studied their decomposition. The Michigan outwash plain site tends to be drier because sandy soil does not hold water as well. In Delaware, I used shells collected from the Delmarva Peninsula and put them in a beech-maple forest on piedmont. Soil pH measured 4.5 at all sites.

In Michigan, I used shells of 7 species: *Anguispira alternata* (Say, 1816) (n = 48), *Discus catskillensis* (Pilsbry, 1896) (n = 18), *Euchemotrema fraternum* (Say, 1824) (n = 8), *Haplotrema concavum* (Say, 1821) (n = 18), *Mesodon thyroidus* (Say, 1816) (n = 18), *Neohelix albolabris* (Say, 1817) (n = 6), and *Novisuccinea ovalis* (Say, 1817) (n = 2). I chose shells that ranged in size from 4 to 25 mm diameter and ranged from the relatively robust and thick-shelled *A. alternata* to the thin and fragile *N. ovalis*. I individually numbered shells with India ink and divided specimens of each species evenly into the 6 replicate bags (3 from each habitat), for example, 8 *A. alternata* in each bag. For species that did not divide evenly by 6 (*e.g.*, *N. ovalis* and *E. fraternum*), I put one remainder in each of the outwash plain and the moraine localities. The Delaware bags each contained 7 *Triodopsis fallax* (Say, 1825).

At the start of the experiment, shells ranged from fresh to eroded and some had been broken by small mammal depredation. The fact that some shells were not fresh at the start is not a problem because I compared relative shell loss from year to year. Although older shells might be expected to decompose more rapidly, for example due to periostracum loss, as will be seen in the results, periostracum loss had no significant effect on percentage annual shell mass loss. The Delaware shells were intact, but most were missing some periostracum at the start of the experiment. In Delaware, I used only one species, *Triodopsis fallax*, which has a fairly robust shell.

The fact that the mesh bags in Michigan and Delaware had no species in common means that I cannot examine species-locality effects among all three localities. However, since I used the same species at both Michigan sites, I can look for species-locality effects there. Because sample sizes of some species were very small, caution should be exercised in interpreting results.

Analyses

To determine shell decomposition, I weighed shells annually after retrieving them from the litter bags, cleaning off adhering soil, and air-drying them to constant mass. Cleaning and drying resulted in little to no observable shell loss although a few small non-adhering pieces of periostracum occasionally fell off shells during drying. I did not retrieve shell fragments less than about 4 mm^2, so shells with these kinds of small fragment losses are interpreted in this study as shell mass loss through decomposition. Larger shell fragments that could be associated with an individual shell were included in the mass measurements of that individual. In addition, in order to examine mass loss by shell breakage and to examine the effect of periostracum loss on decomposition rate, I also annually estimated the proportion of the shell and periostracum that were missing and measured maximum diameter of the remaining shell. I re-inked identification numbers onto the shells if the previous numbers had faded.

I made some adjustments to the data set. In some instances, the apparent mass of a shell increased over a previous year (perhaps a piece of sand had lodged in the shell). For instances in which the mass of a shell increased more than 10%, I removed the increased year from the analysis.

I excluded the first year of *Discus catskilleusis* measurements from the analyses. The shells had been collected alive and dried without removing the bodies. The shells lost much more mass the first year (mean of 5 mg or 46% of shell mass) compared to subsequent years (0.5 mg or 15% of shell mass), suggesting that the soft tissue body masses had been a significant part of the mass the first year. Indeed, Pearce and Gaertner (1996) reported dry mass of *D. catskilleusis* to be about 2 mg. Because soft part decomposition the first year seemed to account for a large portion of the mass loss, I excluded all first-year *D. catskilleusis* from mass loss analysis.

In most analyses, I was interested in the shell mass loss due to non-breakage factors rather than shell loss due to breakage. To focus on effects of dissolution and micro-grazers, I excluded from statistical analyses shells that suffered catastrophic breakage during a particular year. I included shells that were intact for at least 2 contiguous years. I defined broken shells as those that lost more than 15% of shell (estimated visually and recorded annually) or more than 5% shell maximum dimension (measured and recorded annually). Defining shell breakage using the percent shell present was independent of any changes in shell mass.

Although a control was not used in this experiment, for example, to assess repeatability of measurements from year to year, the precision of measurement obtained was much greater than the variation from year to year.

Statistical tests and comparisons

The primary measure I used to assess shell decomposition was decrease in mass over time. In order to standardize so shells of different starting masses could be compared, I calculated % shell mass loss over time and used this measure in comparisons. I used this measure for addressing questions comparing shell decomposition rates among different species and different localities. A test for normality of percent shell mass loss of *Anguispira alternata* showed the data to be kurtotic; sample sizes of the other species were too small to allow tests for normality. Consequently, I transformed the data using Log(x+1) and used ANOVA to compare different species or localities. I used the Tukey test to examine post-hoc differences.

In order to evaluate whether shell decomposition rate increased after periostracum loss, I examined whether shell mass loss rate correlated with percent periostracum loss.

To calculate the half life of the shell, I extrapolated the shell decomposition rate to determine when half the mass would remain.

RESULTS

Examples of shells that had decomposed for 4 and 7 years are shown (Fig. 1). An example demonstrating how the mass changed for individual shells of *A. alternata*, for 3 shells that remained intact, and 3 shells that experienced catastrophic breakage at some point in the 7 year experiment, is shown (Fig. 2).

Shell decomposition rate differed among species in 119 shell specimens that did not break (ANOVA, $F = 3.774$, $P = 0.001$) (Fig. 3). The Tukey post hoc test showed that decomposition rate of intact *Anguispira alternata* was less than that of *D. catskilleusis*, and *M. thyroidus* was less than those of *D. catskillensis, H. concavum,* and *T. fallax*. Interestingly, larger shells had a slower percentage shell mass loss rate than smaller shells (Pearson correlation, $N = 142$, $R^2 = 0.088$, $P < 0.001$, unbroken shells only, not shown). Of the 5 species having at least 10 unbroken specimens, *A. alternata* was the only one showing a significant within-species correlation of shell mass loss with shell size (Pearson correlation, $N = 48$, $R^2 = 0.099$, $P < 0.05$), suggesting that it might be the major contributor to the correlation for all species, although its pattern is not contradicted by the trends in other species. When I subjectively classified *N. ovalis* and *H. concavum* as relatively fragile shells and the rest as relatively robust shells, I saw no striking difference in trends for percent shell mass loss.

Shell decomposition rate did not differ significantly between the moraine site and the outwash plain site for 100 unbroken specimens in Michigan (ANOVA, $F = 2.536$, $P = 0.114$). Because different species decompose at different rates, and the shells in Delaware were different species from those in Michigan, if there were differences between Michigan and Delaware specimens, I would not be able to differentiate species differences and locality differences. Consequently, I omitted Delaware from the analysis comparing shell decomposition rates among localities.

Surprisingly, shells that lost more periostracum did not decompose faster (Pearson correlation, $R^2 = 0.0004$, $P > 0.5$) (Fig. 4). Although all values of mass loss per year greater than 22% had less than 11% periostracum remaining, that apparent greater variability likely reflects the larger statistical sample of shells with little or no periostracum remaining. Furthermore, five species having sample sizes of at least 12 individuals had shell decomposition rates independent of periostracum loss (separate species P-values > 0.2 to > 0.5). Although periostracum loss itself did not affect shell decomposition rate, it varied among species in 113 shells examined (ANOVA, $F = 4.997$, $P<0.0005$) (Fig. 5).

Considering the intact shells only, which decomposed at an average of 6.4% per year, the half life of an individual shell (protected from macro-grazers) would be 11.5 years and after 35.8 years only 10% of the shell would remain. Considering both intact and broken shells, which decomposed at an average of 10.2% per year (Fig. 3), the half life

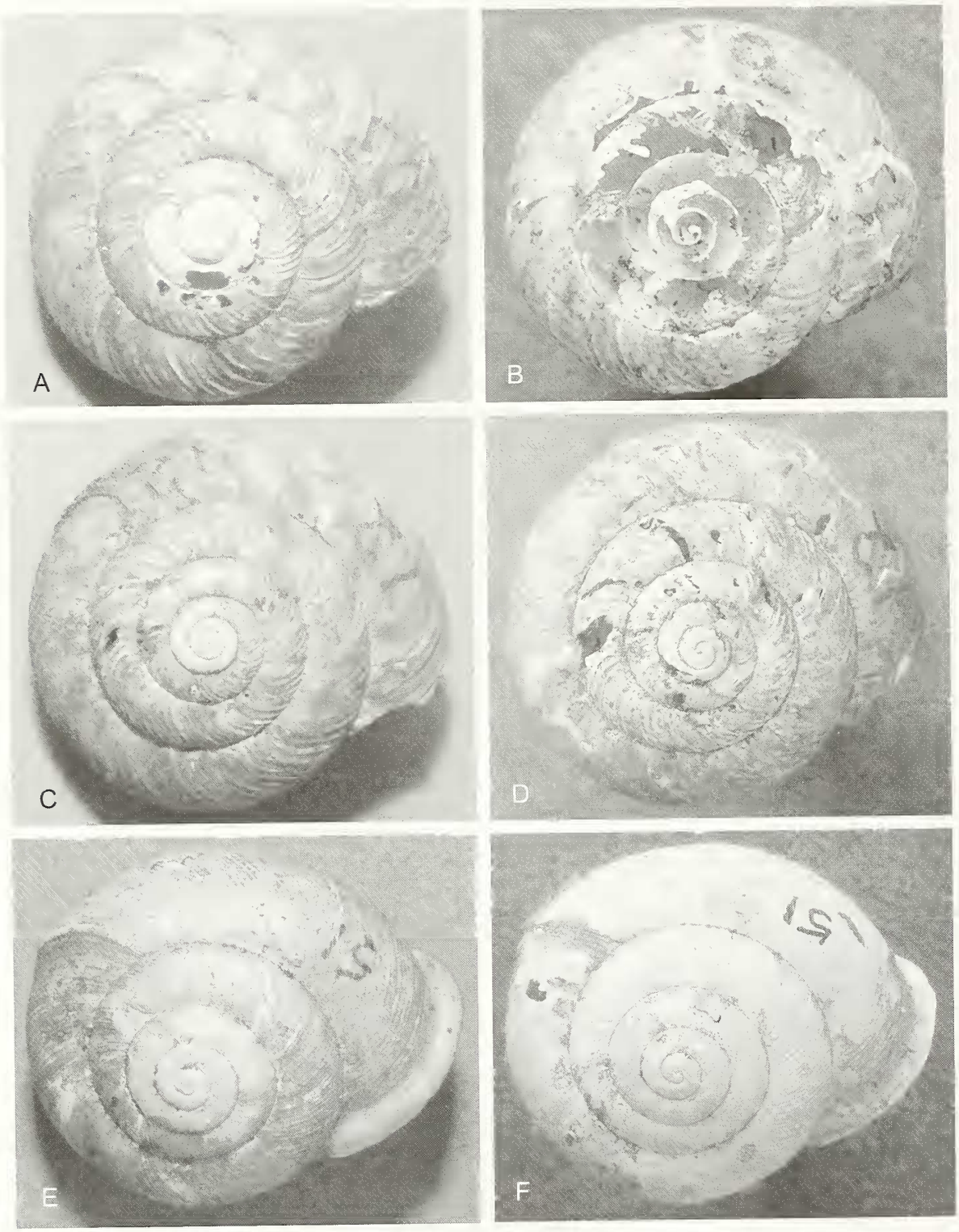

Figure 1. Appearances of three individual shells after 4 years (left column, A, C, E) and 7 years (right column, B, D, F): *Anguispira alternata* No. 03 (13.6 mm diameter; A, B), *A. alternata* No. 12 (17.6 mm; C, D), *Mesodon thyroidus* No. 51 (23.1 mm; E, F).

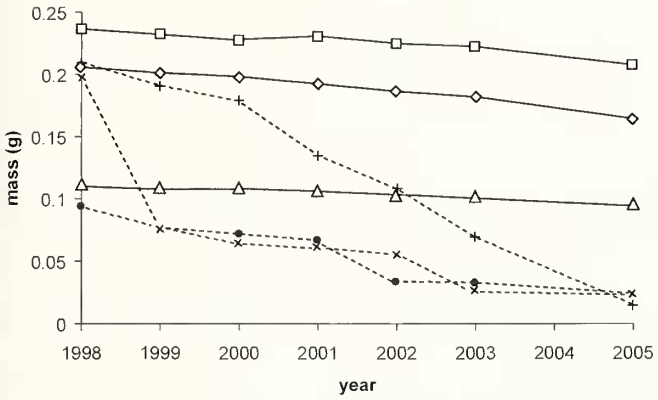

Figure 2. Loss of *Anguispira alternata* shell mass over 7 years. Dashed lines are shells that broke during the experiment; solid lines are shells that remained intact.

of the shell would be 7.5 years; after 22.4 years, only 10% of the shell would remain.

DISCUSSION

Because shells of different land snail species decompose at different rates, these results demonstrate that using shells from dead snails has potential to bias estimates about assemblages of living snails. Admittedly, sample sizes of some species in this study were very small, so results about those species must be interpreted with caution; however, being cautious with those results does not change conclusions about species with larger sample sizes. Conclusions in studies using empty shells should indeed be drawn carefully.

Shell decomposition rates are likely influenced by a plethora of factors. Three of the factors that might influence shell decomposition rates are surface area to mass ratio, shell robustness, and physical and chemical environment. Larger shells, which likely have a smaller surface area to mass ratio, lost mass more slowly than smaller shells in this study. Menez (2002) also found that larger snail shells degraded more slowly. Such a size difference might be expected since shells with a high surface area to mass dissolve more rapidly (Claassen 1998). Although physical and chemical destruction has been reported to be faster in thin-shelled than more robust species (Evans 1972), no effect of shell robustness was observed on shell decomposition rate in this study although a better test for an effect of robustness needs to be conducted. Robustness would be influenced by shell thickness as well as form, such as ridges that add strength; future tests of robustness should examine crush strength among species.

Shell decomposition rates did not differ significantly at two habitats in Michigan, despite the habitats differing in substrate (sandy soil versus poorly sorted moraine deposits), vegetation (relatively low oak and pine with sparser undergrowth versus taller aspen forest with denser undergrowth), and evidently moisture (although the pH did not differ). This result contrasts with leaf litter decomposition rates, which are slower in sandy soil having less moisture and less nutrient-holding capacity (Johnson *et al.* 2000), suggesting that processes regulating leaf litter and shell decomposition might differ. Because temperature, moisture, and pH likely play important roles in shell decomposition, shells in environments different from those I studied are likely to have different decomposition rates. Indeed, Barrientos (2000) found that shells in mesh bags (mesh size not stated) in Costa Rica decomposed in an average of 5 months.

Surprisingly, periostracum did not seem to play a protective role in decomposing shells. Periostracum is usu-

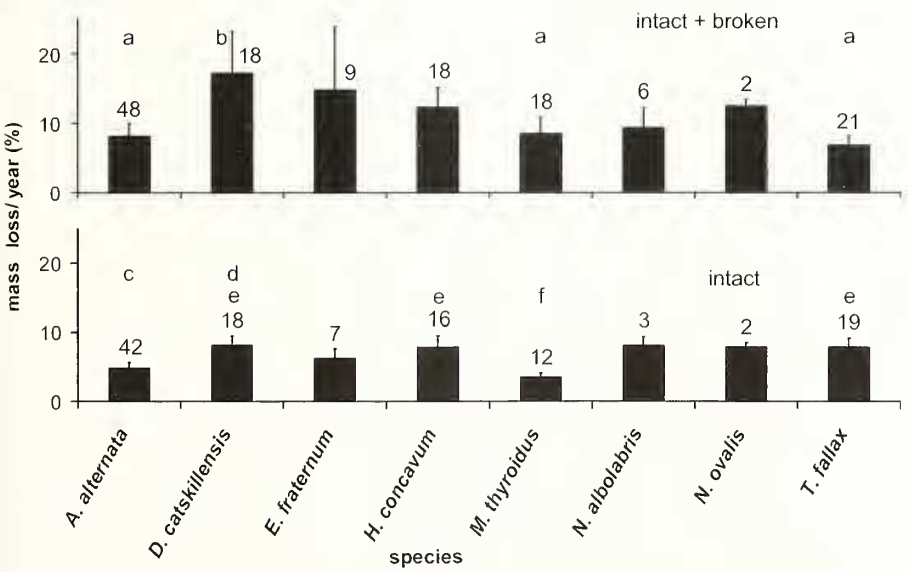

Figure 3. Shell decomposition rate contrasted among species. Lower panel indicates decomposition rate for unbroken shells, upper panel the rate for both broken and unbroken shells together. Numbers above bars indicate initial sample size. Bars with different letters within a horizontal row differed significantly; those without letters did not differ significantly. Data from broken shells were included in the lower graph only for their unbroken duration, which explains unequal mass losses in top and bottom graphs for species having same sample sizes.

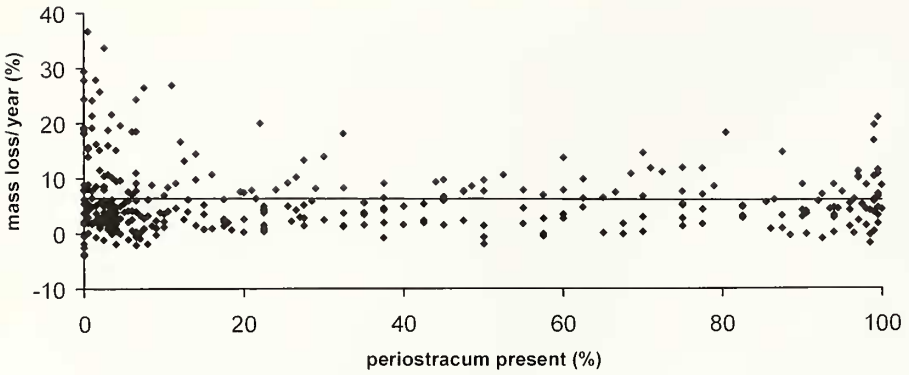

Figure 4. Shells that lost more periostracum did not decompose faster. Points show amount of periostracum remaining at the end of a year (x-axis) and amount of weight loss since the preceding year (y-axis). Individual shells can appear more than once for different years.

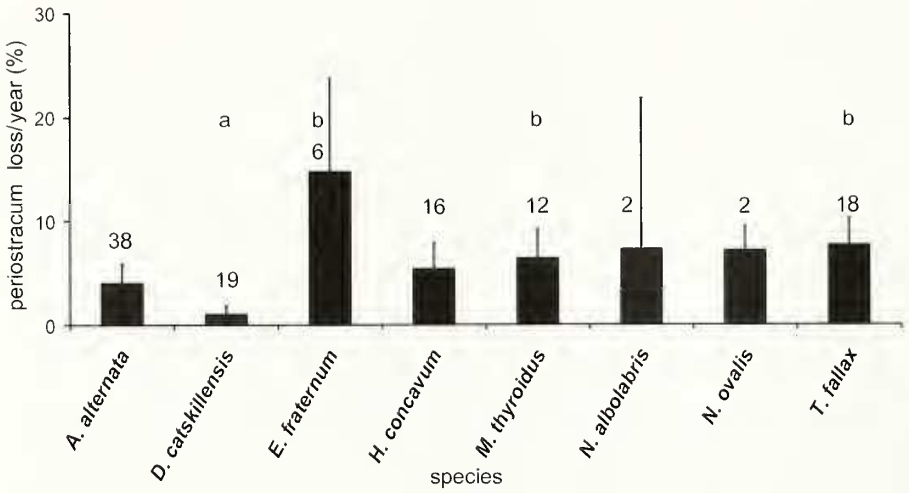

Figure 5. Periostracum loss rate varied among species. Numbers above bars indicate sample size. Bars with different letters within a horizontal row of letters differed significantly; those without letters did not differ significantly.

ally thought to protect shells from boring organisms, erosion, or dissolution by leaf litter acids in terrestrial snails or acidic water in aquatic molluscs (Solem 1974). While most living shells have intact periostracum, the apices of some living shells do erode over time. However, older molluscs missing large areas of periostracum do not seem to suffer serious erosion of the shell, suggesting that water and corrosion proofing qualities of the periostracum may be only of secondary importance (Hunt and Oates 1978). Possibly erosion soon after death starts on the inside surface of the shell, which is not protected by periostracum. Nevertheless, two questions remain: in the present study, why did the shell decomposition rate not increase after the loss of the periostracum, and why does periostracum apparently become more pervious after death, after having stayed intact for years during the snail's life? Regarding the second question, the living snail might behaviorally or chemically maintain a good bond between the periostracum and the shell whereas the bond might weaken after death, allowing ingress of corrosive solutions.

Living snails would be important grazers on decomposing snail shells. Other micro- or meso-organisms that might graze on decomposing shells are likely to exist. In a study of shell mass loss of *Helix aspersa* Müller, 1774 on a dune area in the Netherlands, Cadée (1999) found that shells protected from bioerosion lost about 8% mass in a year, similar to the rate found in this study. However, in that study, shells exposed to bioerosion by other land snails lost mass much more rapidly, 34% in 70 days, indicating that shells exposed to bioerosion could disappear in less than one year. If micrograzers are important contributors to shell decomposition, then the soil conditions (*e.g.*, nutrients) would also be relevant through their effect on the micro-grazers.

Dissolution and chemical conversion are often the main contributors to land snail shell decomposition (Claassen 1998). Colder water can dissolve more calcium carbonate (Claassen 1998) although more rapid dissolution can be expected at higher temperatures, at least in non-saturated water. On one hand, presence of moisture and lower pH increase the speed of shell decomposition (Claassen 1998, Reitz and Wing 1999). On the other hand, alkaline soils rich in calcium retard the breakdown of empty shells (Claassen 1998, Schilthuizen and Rutjes 2001, Cameron *et al.* 2003).

Although influences on decomposition rates of snail shells on forest floors are poorly known, insights might be gained from the more numerous studies on decomposition of leaf litter. Although different processes probably act on shells and leaves, results from studies finding leaf litter decomposition differences among habitats and climates are probably applicable to snail shell decomposition. For example, warmer climates would probably increase decomposition rates of shells, as it does in leaf litter (Bell 1974). In

leaves, factors most important at determining the rate of decomposition are those that regulate microorganism activity: temperature, moisture, nutrients, and energy source (Berg and Ekbohm 1991). If microorganism activity plays a large role in shell decomposition, then shell decomposition rates would also be largely affected by processes regulating microorganism activity.

The result that snail shells of different species have different decomposition rates has important ramifications for studies of endangered species and community analysis. Finding empty shells of an endangered species in habitats similar to those studied here would suggest that the species was living in the area within the last several decades at most. However, the results of this study suggest that for community analysis studies, using empty shells to infer abundances of the assemblage of living individuals might violate the assumption that the death assemblage accurately represents the assemblage of living individuals. Including empty shells could overestimate the abundance of robust species.

In the geographical locations and habitats I studied, and with shells protected from macro-grazers, I extrapolate that shells will decompose to 10% of their former mass after several decades. For practical purposes, *e.g.*, in surveys recovering shells from leaf litter samples, shells missing more than 50% of their former mass might not be findable or identifiable, so shells in these conditions might effectively disappear in 7-12 years, their half life. Half lives would likely be shorter if macro-grazers had access to shells.

Future studies might help tease apart the processes involved in shell decomposition. Exploring the decomposition rates of shells in different environments (and geographic localities) and noting biotic and abiotic influences would help to address the importance of different situations (as has been found in leaf litter decomposition studies) and of scrapers or chemical weathering. Laboratory experiments could more directly evaluate the relative importance of the three decomposition methods and the importance of pH and temperature.

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